A LABORATORY STUDY OF THE RESPONSE TO CURRENT OF JUVENILE ATLANTIC SALMON (SALMO SALAR)

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A Laboratory Study of the Response to Current of Juvenile Atlantic Salmon (*Salmo salar*)

by

© Earl G. Dawe, B.Sc. (Hons.)

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Laboratory experiments were conducted in 1978 on rheotropic behavior of juvenile Atlantic salmon from Placentia Bay, Newfoundland rivers. Experiments were designed to investigate the role of water current in directing migrations and to determine the relative importance of environmental factors which may control migration. Smolts, precocious male parr and autumn immature parr were captured for this purpose during their normal periods of migration. Rheotropic behavior was quantified by exposing subjects to current in an experimental flume. Trials were conducted during spring-summer for smolts and autumn for parr.

For smolts, temperature, light intensity and salinity were selected as experimental variables in a fully crossed experiment. Temperature and time were the only variables in parr experiments. Directional preference, latency of the response and orientation of the downstream response were recorded for all trials.

Downstream was the most prominent directional response for all juveniles. Response latency and orientation of the downstream response were generally in agreement with directional preference. Experimental findings were consistent with field observations from this and other studies.

For smolts, experimental variables interacted in regulating rheotropic behavior. The upstream response occurred significantly more frequently in freshwater than at higher salinities. In freshwater latency of the downstream response was shorter where it occurred most frequently. Negative orientation of the downstream response (active movement with the current) occurred significantly more frequently in freshwater than at higher salinities.

Positive orientation (passive movement) was more common at the higher salinities.

For immature parr downstream was the only directional response displayed. This response was also most common for precocious male parr, but some upstream response also occurred. Northeast River precocious male parr showed significantly more upstream response at 8°C than at 12°C. Also for these precocious males, latency of the downstream response was significantly shorter later in the season and at lower temperatures. Orientation of the downstream response for parr was negative.

Water current may be a directional cue in juvenile Atlantic salmon migrations. Environmental factors probably regulate rheotropic behavior and so control the timing and intensity of migrations.

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INTRODUCTION

Rheotropism in fishes was first described by Lyon (1904). Arnold (1974) in a review of the subject defined rheotropism in fishes as any response a fish may display to current. This could be directly, as a result of stimulation by water flowing over the body of the animal, or indirectly, whereby the fish may respond to visual, tactile or inertial stimuli resulting from displacement of the fish in space. The optomotor response described by Dodson and Young (1977) represents an example of rheotropism stimulated by visual cues in an indirect sense.

Rheotropic behaviour is characterized by two types of response (Emanuel and Dodson 1979). The kinetic response is one whereby fish may move against the current (positive rheotropism) or in the direction of current flow (negative rheotropism). The orientational component is classed as positive if the fish faces into the current. Negative orientation occurs when the fish faces in the direction of current flow or 'downstream'. Positive orientation occurs more frequently for most species of fish.

Field studies have shown that different stages in the juvenile portion of the life history of Atlantic salmon (Salmo salar) display different migration patterns. These migrations are seasonal and involve distinct and different rheotropic responses.

In spring some parr which have reached a critical minimum length undergo smoltification and migrate seaward. However, a high proportion of male parr having reached this minimum length do not smoltify but remain as parr or silvery parr (juveniles undergoing the physiological transformation to smolt condition). They mature in freshwater and take part in spawning. It is

believed that precocious sexual development and smoltification are biologically opposite processes (Evropeytseva 1960). Dalley (1978) found that precocity is high in Newfoundland, especially in Placentia Bay rivers.

It has been reported that an upstream spawning migration of precocious male parr (King 1941, 1947, King et al. 1939, Jones and King 1949, 1950, Vladimirskaya 1958, Saunders and Gee 1964) occurs in autumn associated with spawning. However, Murie (1870), Vladimirskaya (1958), Saunders (1960, 1976), Meister (1962), Pyefinch and Mills (1963), Mills (1964), Saunders and Gee (1964), Elson et al. (1972) have reported that parr migrate downstream in autumn. Saunders (1960, 1976) stated that for Ellerslie Brook and the Northwest Miramichi respectively most of these downstream migrants were mature males. Meister (1962) reported that in a small coastal stream in Maine more smolts migrate in autumn than in spring. Saunders and Gee (1964) believed these autumn migrants were silvery parr rather than true smolts. Similarly autumn-migrating smolts in Scotland reported by Calderwood (1906) may have been silvery parr. Chadwick (personal communication) reported a small autumn downstream migration of parr and smolts in West Brook, Newfoundland. Parr which migrate to the estuary do not smoltify in autumn but may do so the following spring. Some remain in the estuary all year round (Saunders 1960). These autumn migrants are forerunners of the following spring migration, rather than leftovers. This is seen from their age distribution (Meister 1962).

Rheotropic behavior of other salmonids is influenced by environmental factors. Reactions of juvenile Pacific salmon (Oncorhynchus sp.) to water current vary with temperature (Keenleyside and Hoar 1954) and can be reversed by sudden changes in temperature (Hoar 1951, Keenleyside and Hoar

1954). Northcote (1962) has shown that for juvenile rainbow trout (Salmo gairdneri) opposite rheotropic responses at different temperatures result in lakeward movement from both outlet and inlet streams. Brannon (1972) has shown that for sockeye fry (Oncorhynchus nerka) water velocity is the directing factor in lakeward migration whereas light intensity and temperature influence the timing and intensity of responsiveness.

For juvenile Atlantic salmon no studies have been carried out to determine the relative importance of factors which could control rheotropic behavior. From field studies there is information on the relationship between the timing and intensity of smolt runs and environmental factors. Geographic regions vary in the effect of environmental factors on migration, reflecting the extent to which discrete stocks adapt to local conditions. Photoperiod, although known to affect rheotropic behavior of salmonids (Keenleyside and Hoar 1954, Northcote 1958), is less dynamic than other environmental factors. Therefore it is less likely to be associated with annual and geographical variations in the timing of migrations.

Least understood is the relationship of light intensity and temperature in controlling smolt migration. Temperature varies directly with light intensity. White (1939), Saunders (1960), Elson (1962), Mills (1964) and Jessop (1975) cited temperature as the releasing stimulus, migration commencing when the temperature reaches 10°C. However Osterdahl (1968) and Solomon (1978) found that in cold springs migration begins before 10°C, whereas in warm springs migration begins when the temperature is in excess of 10°C. Bakshansky et al. (1976) found that in the majority of cases migration begins at a temperature of about 10°C but a range exists of 7 - 14.3°C at the onset of migration for different rivers and years. Minimum and maximum

temperatures recorded throughout the smolt runs in their survey were 7.7°C and 21.4°C respectively. Dalley (1978) found that for the 1977 Northeast River smolt run migration began at a temperature below 10°C and peak movement occurred when a maximum evening temperature of 9.5°C was reached.

The diel pattern of migration also varies among rivers. White (1939), Swain (1957), Vladimirskaya (1958), and Jessop (1975) reported that smolt migration is mainly nocturnal. Various diurnal patterns of migration also exist (Berry 1933, Hayes 1953, Baglinière 1976, Solomon 1978). Mitans (1967) and Osterdahl (1964, 1968) have described nocturnal movement during the first part of migration, with increased diurnal movement later in the run. Bakshansky et al. (1976) found that in northern rivers migration was most intense in the daytime or in morning and evening. However, in lower latitudes, such as in the Baltic basin, initial descent is nocturnal but migration occurs in the daytime as well during the period of maximum migration. Murray (1968) reported mainly diurnal movement for Little Codroy River, Newfoundland.

Little is known of smolts once they reach the estuary except that they move with the tides and at the same speed (McCleave 1977, Fried et al. 1978, McCleave and LaBar 1976). In bays, smolts change from moving only with the tides and move seaward by stemming flood tides as well (LaBar et al. 1978). Nothing is known of rheotropic behavior in the open ocean.

Also little is known of environmental factors which may affect upstream and downstream autumn migrations of precocious male parr or downstream autumn migration of non-precocious parr. There is some evidence that downstream migration is related to decreasing autumn temperature (Vladimirskaya, 1958). Orton (1942) and Smirnov (1971) reported a relationship between temperature change and spawning time.

Experiments conducted in this study were designed to quantify kinetic and orientational components of the rheotropic response of juvenile Atlantic salmon at three stages in the juvenile portion of its life history; smolt, precocious male parr, and autumn-non-precocious parr.

Furthermore, certain environmental factors were selected for investigation in these experiments to determine their role in observed movements. Temperature was selected for all experiments because of its long-accepted importance in controlling migration of parr and smolts. Light intensity and salinity were also selected for smolt experiments because they vary throughout the duration and course of the smolt run. Moreover, the relative importance of these factors in controlling smolt migration is unclear.

By combining laboratory experiments with field observations the role of potentially important environmental stimuli in regulating rheotropic behavior as a mechanism of migration was investigated.

Two hypotheses were considered for investigation in this study. Firstly, it is hypothesized that water current serves as the directing mechanism in migrations of juvenile Atlantic salmon. Secondly, environmental factors serve as cues, indicating which response (upstream or downstream movement) is appropriate to specific seasonal migrations.

MATERIALS AND METHODS

Apparatus

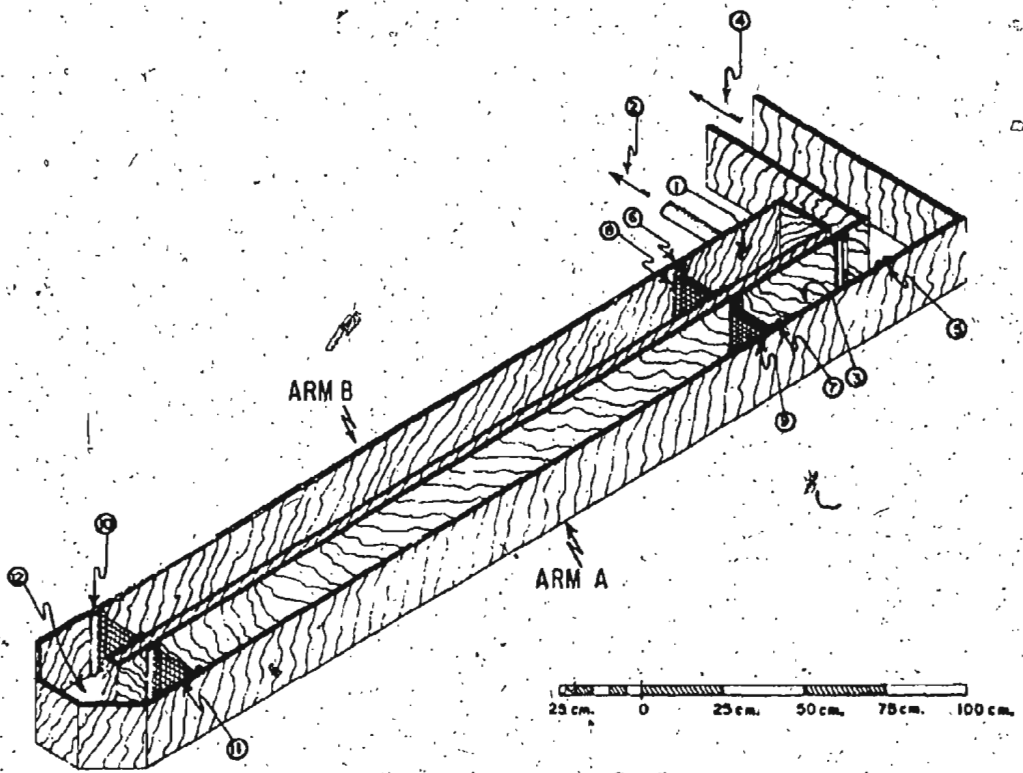
All experiments were conducted using an apparatus designed by the late Dr. C.W. Andrews and modified for this study (Figure 1). The term 'migration channel' has been adopted to describe it, after an apparatus similar in principle used by Brannon (1972). The migration channel was constructed of 1.9 cm plywood. It was 2.78 m long and 38.5 cm wide. Each arm was 15.5 cm wide and 18.5 cm deep.

In this channel the end of either arm (Figure 1) could serve as inflow (1, 3) or outflow (2, 4). When arm A was used as inflow (3) a removable end was put in place (position 5) to close off this arm. A 4.8 cm hole in the floor of the end of arm B then served as the outflow. A plastic pipe 4.8 cm in diameter (2) returned water to a 357 litre catchment basin and a 1/3 h.p. sump pump returned it to the 407 litre reservoir, located directly above. When arm B was used as the inlet (1) a rubber plug was placed in the arm B outlet. The arm A end was removed and the channel served as the outflow (4), returning water directly to the catchment basin.

The inlet received water from the reservoir by gravity flow through a 4.8 cm plastic pipe. A flow control valve in the pipeline was left open during trials. Flexible rubber tubing attached to the inflow pipe allowed water to be directed into either arm.

A wooden partition could be placed in either arm 38 cm above the functional end (positions 5 and 6) to regulate water level and velocity. Fixed galvanized screens were located 3.5 cm below the position of the partition (8 and 9) to retain subjects in the migration channel. Located 206 cm below

Figure 1. Model of migration channel used in experiments on response to current.


ARM B
ARM A
25 cm.
0
25 cm.
50 cm.
75 cm.
100 cm.

these were moveable screens (10 and 11). These confined subjects in the starting position below (12) and were lifted to initiate a trial. The migration channel was enclosed by a green translucent plastic screen. All observations were made through narrow slits.

Experimental Procedure

Subjects were collected by fyke traps from river systems in Placentia Bay. They were immediately transported to a room adjoining that containing the migration channel. There they were kept in 105-120 litre rectangular fibreglass tanks with plexiglass covers and overhead fluorescent lighting. Photoperiods were controlled by an electric timer. During the day period light intensity at the water's surface was constant for each tank but varied from 117 to 581 lux (11-53 ft.c.) among the holding tanks, as measured by a Gossen Lunasix 3 Light Meter. Compressed air was bubbled through an air stone in each tank.

Eight holding tanks were part of two independent recirculating systems. Each system consisted of four tanks through which cooled water flowed. For each system water flowed by gravity from a 1177 litre reservoir into the tanks and through overflows. Water then passed through a glass wool and charcoal filter and into a 120 litre catchment basin. From there it was returned to the reservoir by 1/3 h.p. general purpose pumps. Later, 1/3 h.p. sump pumps were used after the original pumps had broken. Temperature was regulated by cooling coils submerged in each reservoir.

Trials were conducted at acclimation temperature. Temperature in the migration channel was controlled by using water from the appropriate reservoir. Further, water was continuously exchanged by siphons between the holding

reservoir and the experimental reservoir. When necessary, ice was also used. Water level was constant at 12 cm and current velocity was 10 cm/sec. Current velocity was measured by timing the movement of surface and submerged objects in the channel.

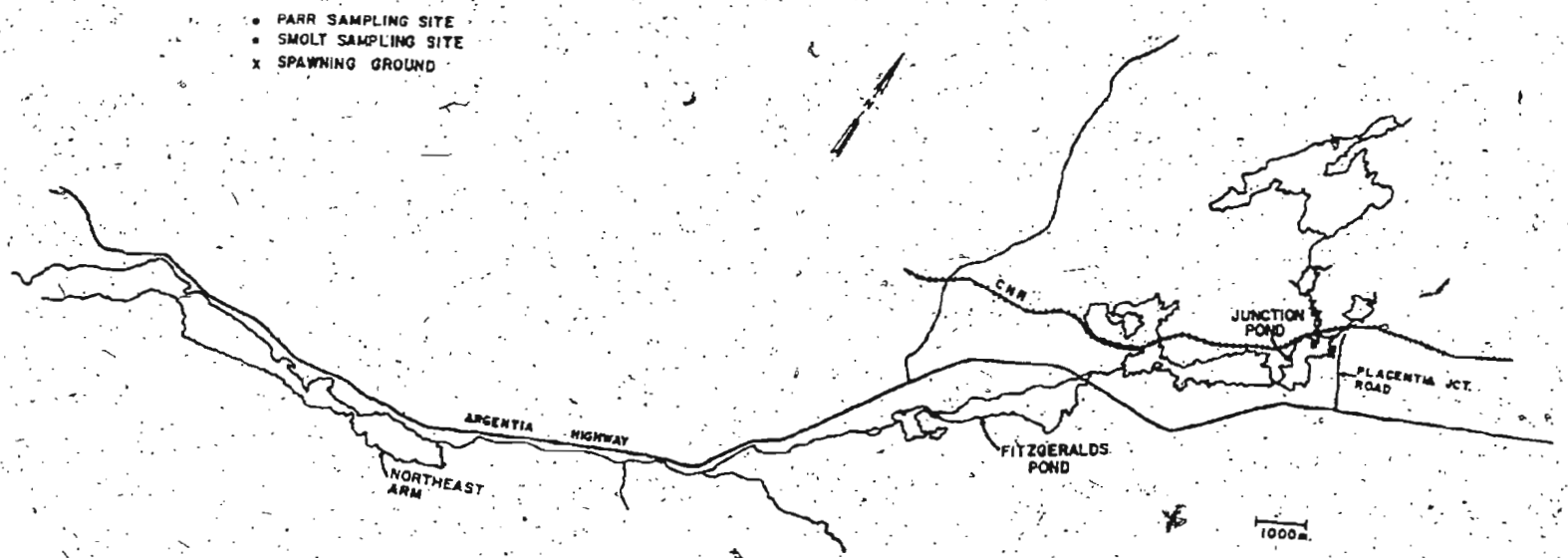
Subjects were run independently in trials and were subjected to repeated trials. They were marked by inserting a piece of colored, plastic-coated copper wire in the caudal fin. In this way individuals were recognized and an inter-trial interval of at least one hour was maintained so that results of any given trial would not be affected by previous experience. Direction of current flow was reversed at random, using a random number table.

A typical trial began by placing a subject in the starting position for five minutes. Then the restraining screens were removed from below and the subject was free to move upstream or downstream. A response was recorded if the subject moved one meter in either arm. Observations were made on three components of the response; directional preference (upstream or downstream movement), orientation and latency. A stopwatch was used to measure latency of the response (the time between liberation and reaching a one meter mark). If no response occurred within ten minutes the trial was terminated and the subject was returned to the holding tank.

Smolts

Experiments on smolts from the 1978 Northeast River smolt run were conducted from May 14 to July 14. Samples of 48, 36 and 28 smolts were taken from the outlet of Fitzgerald's Pond (Figure 2) on May 14, May 24 and May 30-31 respectively. Samples were held at different salinities (0 o/oo, 15 o/oo and 33 o/oo for the three successive sampling periods respectively). Photoperiod was 16 hours of light each day and subjects

Figure 2. Northeast River system showing locations of sampling sites.


• PARR SAMPLING SITE
• SMOLT SAMPLING SITE
x SPAWNING GROUND
CNR
JUNCTION POND
PLACENTIA JCT. ROAD
ARGENTIA HIGHWAY
NORTHEAST ARM
FITZGERALDS POND
1000m

were given at least two days to acclimate to holding conditions before trials began. The 15 o/oo salinity was obtained by diluting seawater (33 o/oo) obtained from the Marine Sciences Research Laboratory, Logy Bay.

Initial trials were conducted on recently captured smolts at acclimation salinity. This was to initially quantify the downstream response and to control for further experiments on these smolts held a longer time in captivity. Smolts were subjected to a maximum of four trials each. Trials were conducted at 10°C and dim light intensity. Dim light intensity was obtained from two 40-watt incandescent bulbs situated equidistant on either side of the starting position and outside the screening. At the water's surface, light intensity ranged between 0.7 and 1.9 lux (0.064 - 0.17 ft.C.) along the length of the migration channel. Trials at each salinity were completed within five days. No difference in response due to repeated trials or length of time in captivity was observed.

Further smolt trials were run to determine the effect of light intensity, temperature and salinity on response to current in a fully crossed experiment. The subjects of this experiment were 20 smolts retained from previous 0 o/oo and 15 o/oo trials. Some were held as long as one month in captivity.

Trials at successive salinities of 0 o/oo, 15 o/oo and 33 o/oo extended from June 13 to July 14. Within salinities, subjects were held first at 10°C, then at 15°C. Subjects were acclimated to each temperature change for 2 days before trials commenced. Trials were

conducted at acclimation temperature and both dim and ambient light intensity for each temperature. Dim light intensity was as described for the initial smolt experiment. Ambient light intensity was obtained by turning on an overhead fluorescent light. This gave a light intensity at the water surface which approximated that in the holding tanks, ranging from 145 to 465 lux (13 - 43 ft.C.) along the length of the migration channel. This was similar to normal daylight conditions.

Paired trials were conducted for each smolt, one at each light intensity. Order of light intensity within each pair was determined using a random number table. Each smolt was subjected to three pairs of trials at both temperatures for the three successive salinities. For each subject a one-hour interval was maintained between successive pairs of trials. Intervals were of four days duration before first trials at a new set of experimental conditions. These measures were taken to maintain independence of results from repeated trials. Two casualties incurred during this experiment were replaced by smolts which had been used in initial 33 o/oo trials. These had been held at the Marine Sciences Research Laboratory in freshwater, under 16 hours of light each day and with ambiently varying temperature. Despite these conditions, results from the two replacements did not differ from those of other subjects.

Field observations on 1977 smolt runs were obtained from Dalley (1978) for Northeast River and O'Connell and Andrews (unpublished) for Southeast River and its tributary, Beaver River. These observations included records of daily counts of smolts captured in fyke traps which were set in the river. Sometimes, especially at the time of mass migration, traps were checked in the morning and evening. Otherwise they were checked in the morning only. Daily morning temperatures were also recorded.

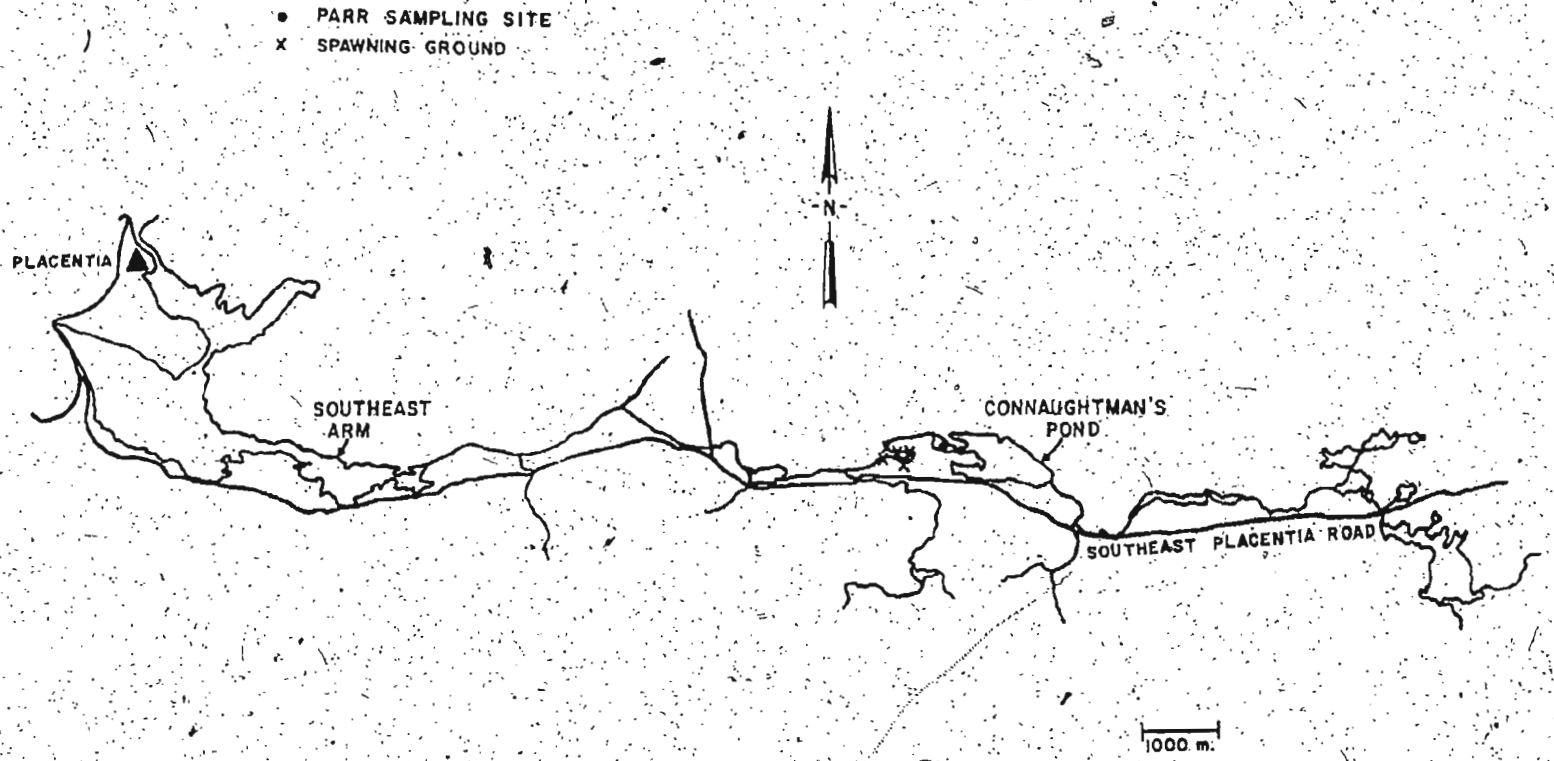
Parr

Experiments were conducted on parr in autumn 1978. Parr used in this study were held under a 12:12 light-dark photoperiod. Each sample was divided between a control and an experimental group. Subjects were acclimated to holding conditions for at least 17 hours before trials commenced. Trials were conducted at ambient light intensity alone. Control and experimental groups were run on alternate days. Parr were subjected to three trials each, following which they were killed and examined for sex and maturity.

Parr were taken from Junction Pond near the inlet of Northeast River (Figure 2) from September 19 to November 8. All were later found to be ripe precocious males. For each sample half was held at 12°C (the control group) and half at a temperature which decreased with each successive sample (the experimental group). Decreases were of 2°C except for the last sample, for which a decrease of only 1°C could be achieved. Samples were of 10 parr for initial 12°C trials and 20 for all other samples except the last. For trials at 5°C and controls, sample size was 40.

On October 29 a sample of 40 parr was taken from Connaughtman's Pond near the outlet of Southeast River (Figure 3). Of these 20 were held and tested at 5°C while 20 served as controls. The control group was maintained and tested at 12°C. On dissection following trials eight were found to be precocious males and 32 were immature parr, all but three of which were females.

Figure 3. Southeast River system showing location of parr sampling site.


• PARR SAMPLING SITE
x SPAWNING GROUND
N
PLACENTIA
SOUTHEAST ARM
CONNAUGHTMAN'S POND
SOUTHEAST PLACENTIA ROAD
1000 m.

Statistical Analysis

Data from the second smolt experiment involving response, light intensity, temperature and salinity were analyzed using a 4-dimensional contingency table (Fienberg 1970, 1977). A computer program provided by Dr. J. Rice (after Fienberg 1970) was used to estimate expected cell values for each proposed model by an iterative procedure. It also calculated the likelihood ratio chi-square statistic for each model. Using the procedure described by Fienberg (1977) the model which showed the significant interactions was selected. The 3 x 2 x 2 x 3 contingency table was then partitioned according to Fienberg (1970) to show the effects of the significant interactions.

Latency of the response for this smolt experiment was analyzed using a 4-factor analysis of variance with unequal replication. Values for latency were converted to $\log_{10}$ for this purpose and the analysis of variance was performed by a computer program contained in SPSS (Statistical Packages for the Social Sciences). This program computed F values for the main effects as well as for all possible interactions. It also assigned a significance level to each F value. A table was drawn to show the mean latency at all combinations of experimental factors. This table was then partitioned to show the effects of the significant interactions.

Other statistical tests involved determining whether responses which fell into two mutually exclusive categories followed an expected distribution. The binomial distribution was used to determine the probability that observed distributions did not differ significantly from a random distribution ($P = 0.5$) (Zar 1974). In this way it was used as a test of significance for up vs down in assessing directional preference for the initial smolt experiment as well as for experimental and control groups of Northeast River precocious male parr,

and Southeast River parr. It was also used in this manner to test for significance in differences between positive and negative orientation of the downstream response for the second smolt experiment as well as for experimental and control groups in both parr experiments. The binomial was further applied to test the significance of an observed difference between two sets of experimental conditions for a given response. In this case P (equal to the number of a given response per number of trials) for one set of experimental conditions was considered to be the expected distribution. The binomial was then used to determine if the frequency of this response at another set of experimental conditions did not differ significantly from the expected. In this way, it was used in the initial smolt experiment to test for significance in the difference of the upstream response between two salinity regimes. In the same manner it was also used to test for a significant difference in the upstream response between two treatment levels of the experimental groups for both parr experiments.

Response latency for Northeast River precocious male parr was analyzed by least squares regression for both up and down responses. Log_{10} latency was regressed on temperature for experimental groups and on day of capture for controls. For each regression there were multiple values of Y for each X. Significance of each regression was tested by analysis of variance according to Zar (1974).

For Southeast River precocious male parr and non-precocious parr the students' t-test was used to test for significance. Tests on log_{10} latency compared experimental and control groups for the downstream response. For the precocious male experimental group the significance of the difference

between up and down was also tested. For all statistical tests, results were accepted as being significant based on $P < 0.05$.

All regressions and t-tests were performed using programs for an Olivetti Underwood Programma 101 Desk Top Calculator.

RESULTS

Kinetic component

Smolts

Directional preference:

Of the two directional responses, downstream was the more prominent at all salinities ($P < 0.001$, Table 1). The upstream response occurred most frequently in freshwater (9%). The difference in the proportions of upstream response between 0 o/oo and 15 o/oo was very highly significant ($P < 0.001$). The proportion of no response was high at all three salinities (58 - 76%).

Directional preference of smolts from the second experiment is presented in Table 2 in the form of a contingency table. All three 3-factor interactions involving response were important in determining the observed distribution of responses (Table 3). Light intensity and salinity interacted in influencing direction of movement as did light intensity and temperature. Temperature and salinity also interacted with response. All possible 2-factor interactions were important, as were all main effects. Possible interactions shown not to be significant by this model are the 4-factor interaction and the light intensity-temperature-salinity interaction.

Interactions:

Ambient light intensity and the higher temperature interacted to produce the greatest occurrence of the downstream response (99, Table 4a). Also under these conditions was the lowest occurrence of the no response component (40). At the other extreme, dim light intensity and the lower

Table 1. Direction of movement of newly-captive Atlantic salmon smolts exposed to current, using replicate trials. (Percentage in parentheses)

Salinity	Response				No. of trials	No. of subjects
	Up	Down	P	No Response		
0 o/oo	10 (9)	38 (33)	P < 0.001	67 (58)	115	48
15 o/oo	0 (0)	27 (25)	P < 0.001	81 (75)	108	36
33 o/oo	1 (1)	23 (23)	P < 0.001	74 (76)	98	28
Total	11	88		222	321	112

P< 0.001 (Difference in upstream response between freshwater and 15 o/oo, using the binomial test.)

Table 2. Effect of light intensity, temperature and salinity on direction of movement of Atlantic salmon smolts exposed to current.

Salinity		0 o/oo		15 o/oo		33 o/oo		Total[1] No. of trials
Light Intensity		Dim	Ambient	Dim	Ambient	Dim	Ambient	
Temperature	Response							
10°C	Up	16	13	10	16	8	7	70
	Down	25	31	16	18	21	28	139
	No Response	19	16	34	26	31	25	151
15°C	Up	16	18	15	8	14	15	86
	Down	25	25	24	39	26	35	174
	No Response	19	17	21	13	20	10	100
Total No.[1] of trials		120	120	120	120	120	120	720

[1]Each of 20 smolts was subjected to three trials for each combination of experimental variables.

Table 3. Results of 4-dimensional contingency table analysis of direction of movement of Atlantic salmon smolts.

Component Due To	Statistic	df
Model 1	G (1) = 5.2494	4
Difference between models 1 and 2	G (2)-(1) = 0.2313	6
Model 2	G (2) = 5.4807	10
Difference between models 2 and 3	G (3)-(2) = 14.9046	0
Model 3	G (3) = 20.3853*	10

* $P < 0.05$

R - Response
L - Light
T - Temperature
S - Salinity

Models:

(1) RLT + RLS + RTS + LTS

(2) RLT + RLS + RTS

(3) RLT + RLS + TS

Conclusion:

Accept Model (2)

Table 4a. Direction of movement of Atlantic salmon smolts (from table 2) combined by salinity to show response-light-intensity-temperature interaction.[1]

Light Intensity		Dim	Ambient
Temperature	Response		
10°C	Up	34	36
	Down	62	77
	No Response	84	67
15°C	Up	45	41
	Down	75	99
	No Response	60	40

[1]Counts are from replicate trials on 20 smolts (three trials each at each combination of experimental variables).

temperature interacted to give the lowest number of downstream responses (62) and the highest occurrence of no responses (84). Also occurring under these conditions was the lowest number of upstream responses (34).

Ambient light intensity was associated with a greater occurrence of the downstream response than was the higher temperature. This is seen in that the difference between upstream and downstream response was greater for ambient light intensity and the lower temperature (41) than for the dim light intensity and 15°C (30). Comparison of each response between 10°C and 15°C shows that the higher temperature was associated with an approximately proportional increase in upstream and downstream responses. This occurred at the expense of the no response component. Comparison of each response between dim and ambient light intensity shows that ambient light intensity was associated with greater downstream response at the expense of the no response component. Meanwhile the upstream component did not change appreciably.

Light intensity and salinity interacted to give greatest occurrence of the downstream response at ambient light intensity and 33 o/oo (63, Table 4b). The upstream response was lowest at 33 o/oo and both light intensities (22), whereas it was highest at the dim light intensity and 0 o/oo (32). The occurrence of the upstream response decreased continuously with increasing salinity for both light intensities.

For the ambient light intensity the downstream response increased as the upstream response decreased. Although this was not seen for the dim light intensity, the difference between the upstream and downstream response in dim light was greatest at 33 o/oo. For both light intensities the upstream response was highest and no response lowest at 0 o/oo.

Table 4b. Direction of movement of Atlantic salmon smolts (from table 2) combined by temperature to show response-light intensity-salinity interaction.[1]

Salinity		0 o/oo	15 o/oo	33 o/oo
Light Intensity	Response			
Dim	Up	32	25	22
	Down	50	40	47
	No Response	38	55	51
Ambient	Up	31	24	22
	Down	56	57	63
	No Response	33	39	35

[1] Counts are from replicate trials on 20 smolts (three trials each at each combination of experimental variables).

Temperature and salinity interacted to give greatest downstream response at 15°C and 15 o/oo (63, Table 4c). Downstream response was lowest at 10°C and 15 o/oo (34). The upstream response was highest at 15°C and 0 o/oo (34) but lowest at 10°C and 33 o/oo (15). For 0 o/oo there was greater downstream response and lower no response at the lower temperature. However, for the higher salinities there were more downstream responses and fewer no responses at 15°C.

This shows that the effect of temperature varied with salinity. At 0 o/oo the lower temperature was associated with a greater proportion of the downstream response. However at 15 o/oo proportionately more downstream response occurred at 15°C. At 33 o/oo the higher temperature was associated with a proportional increase in both directional responses.

The greatest proportion of the upstream response occurred in freshwater where the no response component was lowest. Increase in salinity was associated with an increase in the proportion of downstream response to upstream response.

Latency:

Means of latencies and of their $\log_{10}$ values for all combinations of experimental conditions are presented in Table 5. Results of analysis of variance on $\log_{10}$ latency are also shown. Tables 6 a-c present data from Table 5 partitioned to show the effects of the important interactions. Three 2-factor interactions were significant ($P < 0.05$), all of which involved salinity.

Table 4c. Direction of movement of Atlantic salmon smolts (from table 2) combined by light intensity to show response-temperature-salinity interaction.[1]

Salinity		0 o/oo	15 o/oo	33 o/oo
Temperature	Response			
10°C	Up	29	26	15
	Down	56	34	49
	No Response	35	60	56
15°C	Up	34	23	29
	Down	50	63	61
	No Response	36	34	30

[1] Counts are from replicate trials on 20 smolts (three trials each at each combination of experimental variables).

Table 5. Mean latency of the response (sec.) of Atlantic salmon smolts to current and the effect of light intensity, temperature, and salinity. (Means of $\log_{10}$ values and no. of observations in parentheses.)[1]

		Salinity					
		0 o/oo		15 o/oo		33 o/oo	
Light Intensity		Dim	Ambient	Dim	Ambient	Dim	Ambient
Temperature	Response						
10°C	Up	219.6 (2.1310) (16)	173.7 (1.9676) (13)	223.6 (2.0887) (10)	163.9 (2.0219) (15*)	211.7 (2.0885) (8)	125.2 (1.8754) (7)
	Down	218.1 (2.0701) (25)	92.7 (1.7154) (31)	202.1 (2.2129) (16)	193.1 (2.0965) (18)	246.3 (2.2627) (21)	209.1 (2.2103) (28)
15°C	Up	275.6 (2.2074) (16)	115.7 (1.8667) (18)	174.5 (1.9540) (15)	163.0 (2.0801) (8)	143.6 (1.9942) (14)	81.8 (1.7185) (15)
	Down	229.5 (2.1924) (24*)	157.3 (1.9789) (25)	192.5 (2.1385) (24)	238.5 (2.1826) (39)	190.0 (2.1253) (26)	138.6 (2.0170) (35)

[1] Means were derived from replicate trials on 20 smolts (three trials each at each combination of experimental conditions).

* N is one less than the total no. of observations since latency could not be accurately recorded for one trial.

Table 5 cont'd.

Results of Analysis of Variance on Log_{10} Latency, N = 467 (sum of upstream and downstream movements less two trials for which latency was not recorded).

Source of variance	Sum of Squares	df	Mean Square	F
Main Effects	4.336	5	0.867	4.243***
Salinity	1.114	2	0.557	2.726
Temperature	0.010	1	0.010	0.048
Light	2.396	1	2.396	11.724***
Direction	1.013	1	1.013	4.957*
2-Way Interactions	5.242	9	0.582	2.849**
Salinity x temperature	1.641	2	0.820	4.014*
Salinity x light	1.420	2	0.710	3.473*
Salinity x direction	1.343	2	0.672	3.286*
Temperature x light	0.030	1	0.030	0.145
Temperature x direction	0.197	1	0.197	0.964
Light x direction	0.027	1	0.027	0.130
3-Way Interactions	0.811	7	0.116	0.567
Salinity x temperature x light	0.245	2	0.123	0.600
Salinity x temperature x direction	0.271	2	0.136	0.663
Salinity x light x direction	0.207	2	0.104	0.507
Temperature x light x direction	0.085	1	0.085	0.417
4-Way Interactions	0.158	2	0.079	0.386
Salinity x temperature x light x direction	0.158	2	0.079	0.386
Explained	10.547	23	0.459	2.244***
Residual	90.546	443	0.204	
Total	101.093	466	0.217	

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 6a. Latency of the directional responses in seconds (from table 5) combined by light intensity and response to show the temperature-salinity interaction. (Means of $\log_{10}$ values in parentheses.)

Temperature	Salinity		
	0 o/oo	15 o/oo	33 o/oo
10°C	165.86 (1.9365)	193.29 (2.1078)	212.45 (2.1757)
15°C	191.96 (2.0604)	207.48 (2.1209)	144.76 (1.9950)

Table 6b. Latency of the directional responses in seconds (from table 5) combined by temperature and response to show light intensity-salinity interaction. (Means of $\log_{10}$ values in parentheses.)

Light Intensity	Salinity		
	0 o/oo	15 o/oo	33 o/oo
Dim	233.13 (2.1455)	195.49 (2.1066)	200.24 (2.1362)
Ambient	128.13 (1.8601)	206.75 (2.1229)	150.70 (2.0163)

Table 6c. Latency of the directional responses in seconds (from table 5) combined by temperature and light intensity to show response-salinity interaction. (Means of $\log_{10}$ values in parentheses.)

Response	Salinity		
	0 o/oo	15 o/oo	33 o/oo
Up	194.67 (2.0411)	179.50 (2.0243)	131.99 (1.8984)
Down	169.21 (1.9716)	212.69 (2.1607)	189.26 (2.1387)

Temperature and salinity interacted to give faster response at 10°C for 0 o/oo and 15 o/oo (Table 6a). At 33 o/oo response was faster at 15°C.

Light intensity and salinity interacted to give a smaller response latency at ambient light intensity for all salinities except 15 o/oo, where the difference was smallest (Table 6b). Overall response at ambient light intensity was significantly faster than in dim light ($P < 0.001$, Table 5).

Downstream response was the faster at 0 o/oo, whereas at 15 o/oo and 33 o/oo the upstream response was faster (Table 6c). Overall the upstream response was significantly faster ($P < 0.05$, Table 5). The fastest downstream response at 0 o/oo occurred at 10°C and ambient light intensity (1.7154, Table 5).

Field observations:

Figures 4-6 show daily smolt counts and morning temperatures for Northeast River, Beaver River and Southeast River respectively. For all three rivers daily catches were small early in the season. The first major increase in daily smolt counts occurred May 12 for Northeast River and Southeast River and May 14 for Beaver River. This was associated with a temperature of 6°C. Overnight rain May 11 was also associated with relatively high May 12 catches. However, May 15 catches, following overnight rain showed a prominent increase only for Northeast River (Figure 4). May 15-16 catches for Southeast River were incomplete as water broke over the trap. Low May 16-20 catches for

Figure 4. Number of smolts captured each day during the smolt run, Northeast River, 1977.

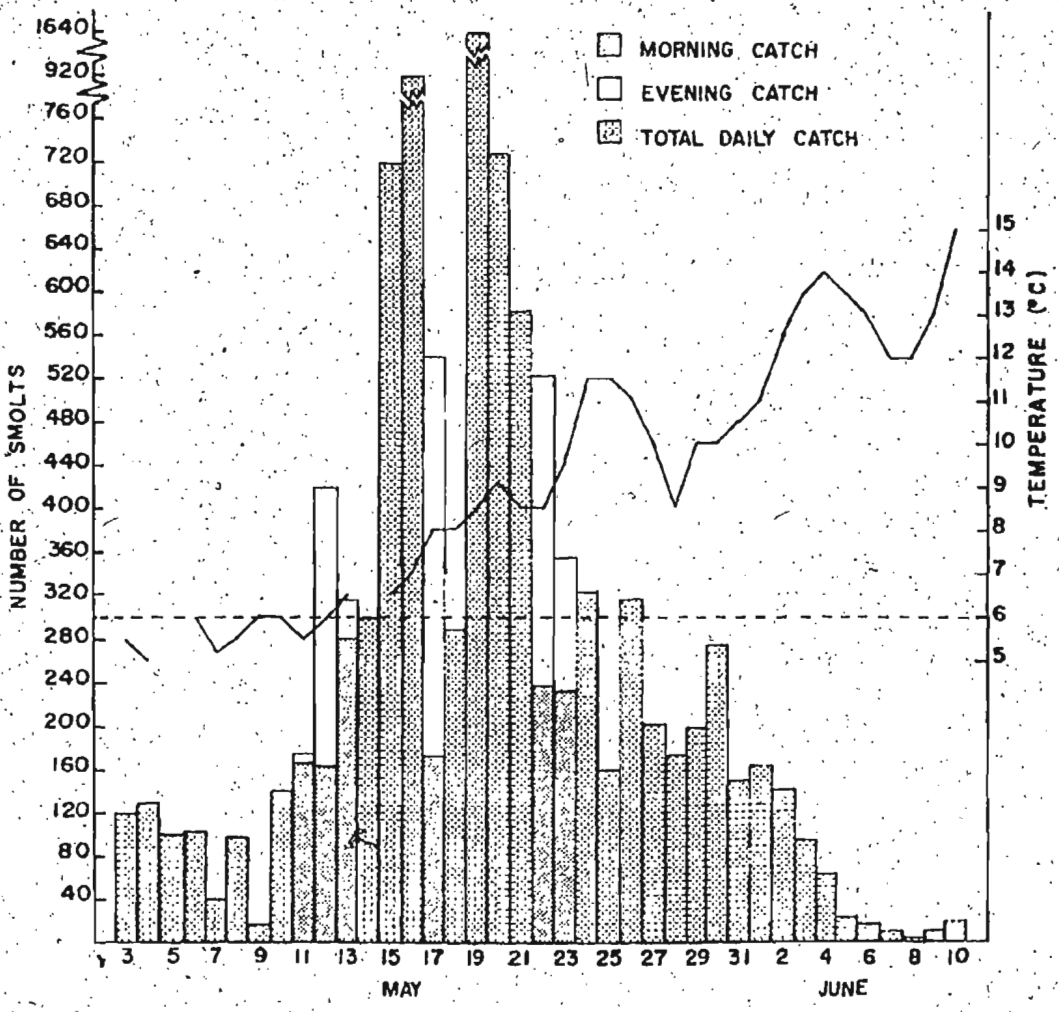
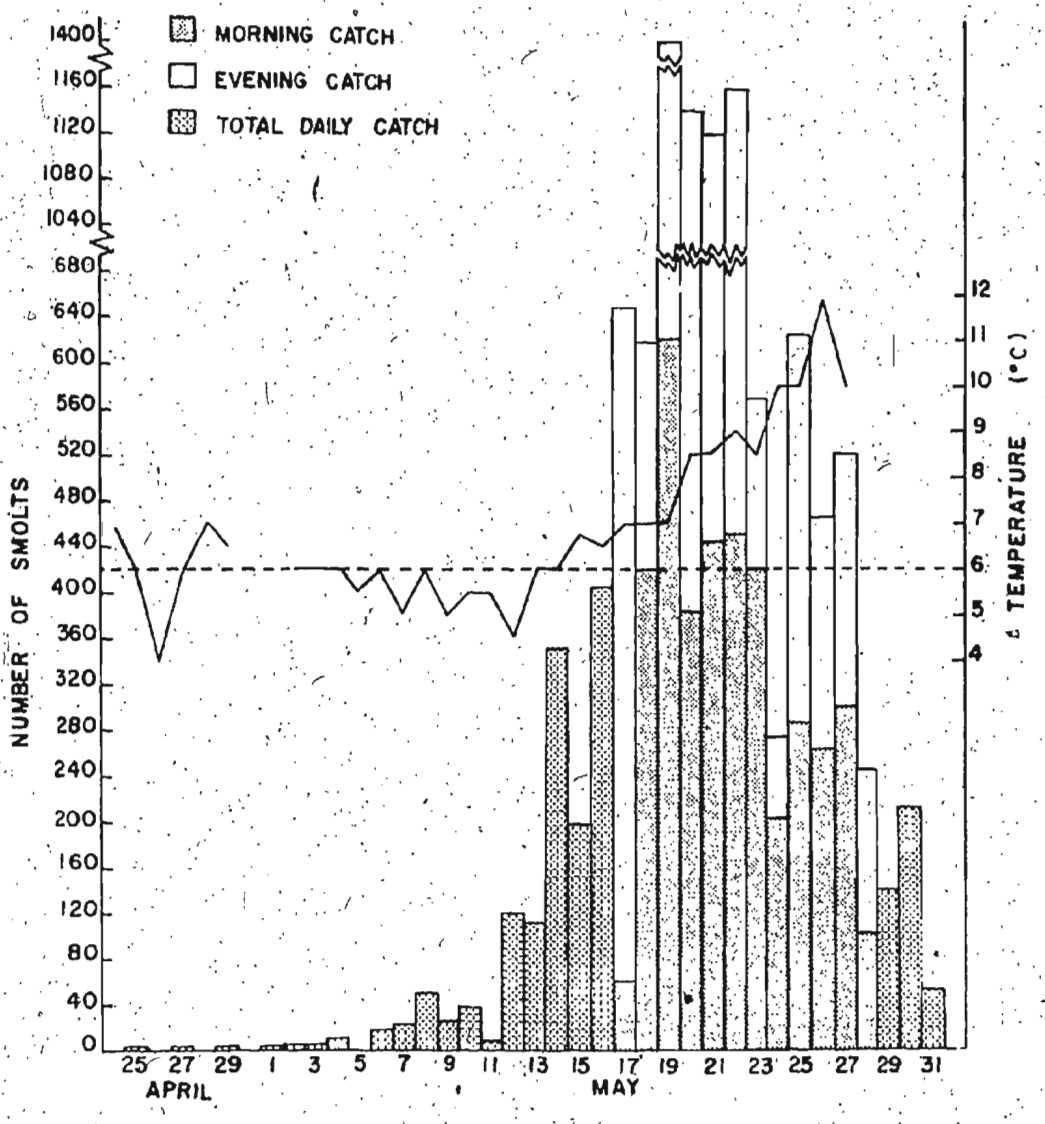

MORNING CATCH
EVENING CATCH
TOTAL DAILY CATCH
NUMBER OF SMOLTS
TEMPERATURE (°C)
1640
920
760
720
680
640
600
560
520
480
440
400
360
320
280
240
200
160
120
80
40
15
14
13
12
11
10
9
8
7
6
5
3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 2 4 6 8 10
MAY
JUNE

Figure 5. Number of smolts captured each day during the smolt run, Beaver River, 1977.


MORNING CATCH
EVENING CATCH
TOTAL DAILY CATCH
NUMBER OF SMOLTS
1400
1160
1120
1080
1040
680
640
600
560
520
480
440
400
360
320
280
240
200
160
120
80
40
0
TEMPERATURE (°C)
12
11
10
9
8
7
6
5
4
25 27 29 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
APRIL
MAY

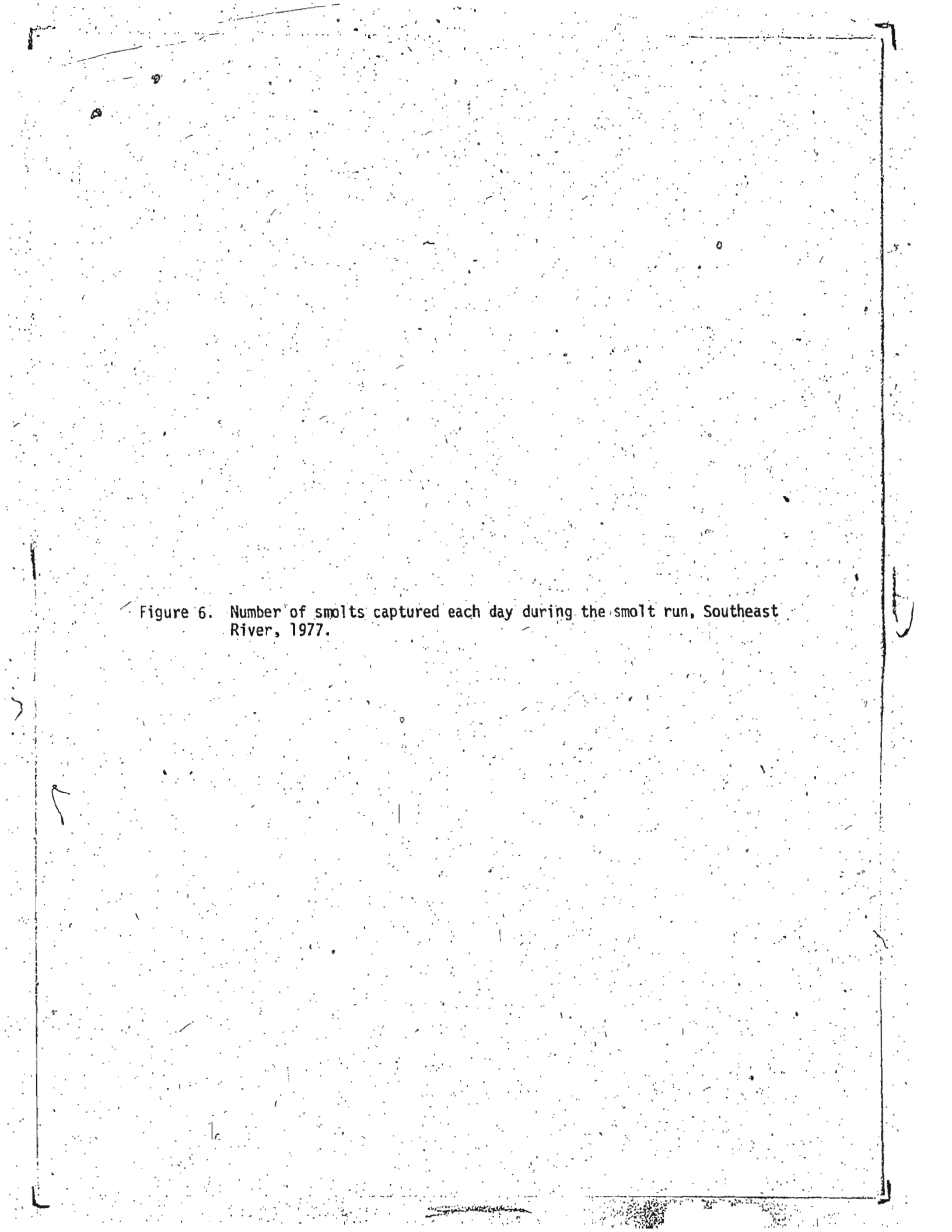
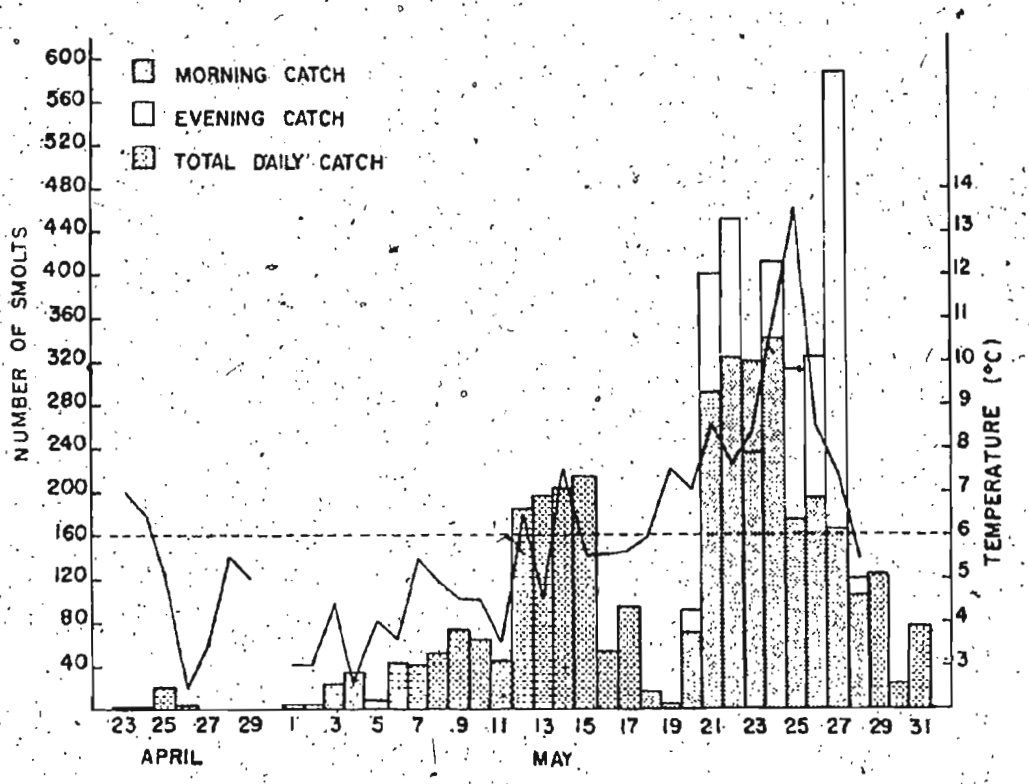


Figure 6. Number of smolts captured each day during the smolt run, Southeast River, 1977.


MORNING CATCH
EVENING CATCH
TOTAL DAILY CATCH
NUMBER OF SMOLTS
TEMPERATURE (°C)
600
560
520
480
440
400
360
320
280
240
200
160
120
80
40
14
13
12
11
10
9
8
7
6
5
4
3
23 25 27 29 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
APRIL
MAY

Southeast River occurred after temperatures dropped below 6°C (Figure 6). High catches were not recorded again until the temperature rose to 8.5°C. Number of smolts fluctuated daily, as did temperature. There was no apparent relationship between actual values of temperature or temperature change and number of smolts. The smolt runs peaked May 19 at 8.5°C and 7.2°C for Northeast River and Beaver River respectively. Day to day temperature was increasing. For Southeast River it peaked May 27 at 7.5°C as temperature was on the decrease.

Traps were checked twice daily at the period of mass migration for Beaver River and Southeast River. For Northeast River evening checks were made only for some days within this period. For all three rivers, especially Beaver River, evening counts outnumbered morning counts mainly for those days closest to peak migration and where daily totals were largest. Earlier and later in the run, or where daily totals were smaller, morning catches were greater. For Southeast River the evening catch was the larger only for the day of peak migration.

Parr

Northeast River precocious males:

Directional preference. For experimental groups the downstream response was significantly the more frequent at all temperatures except 8°C and 6°C (Table 7, Figure 7). This response was also significant for all control groups, with the exception of the October 26-29 group. For the two directional responses the proportion of upstream response increased steadily from 0 % at 12°C to 33 % at 8°C for the experimental groups. It declined steadily beyond 8°C. This increase to 8°C was very

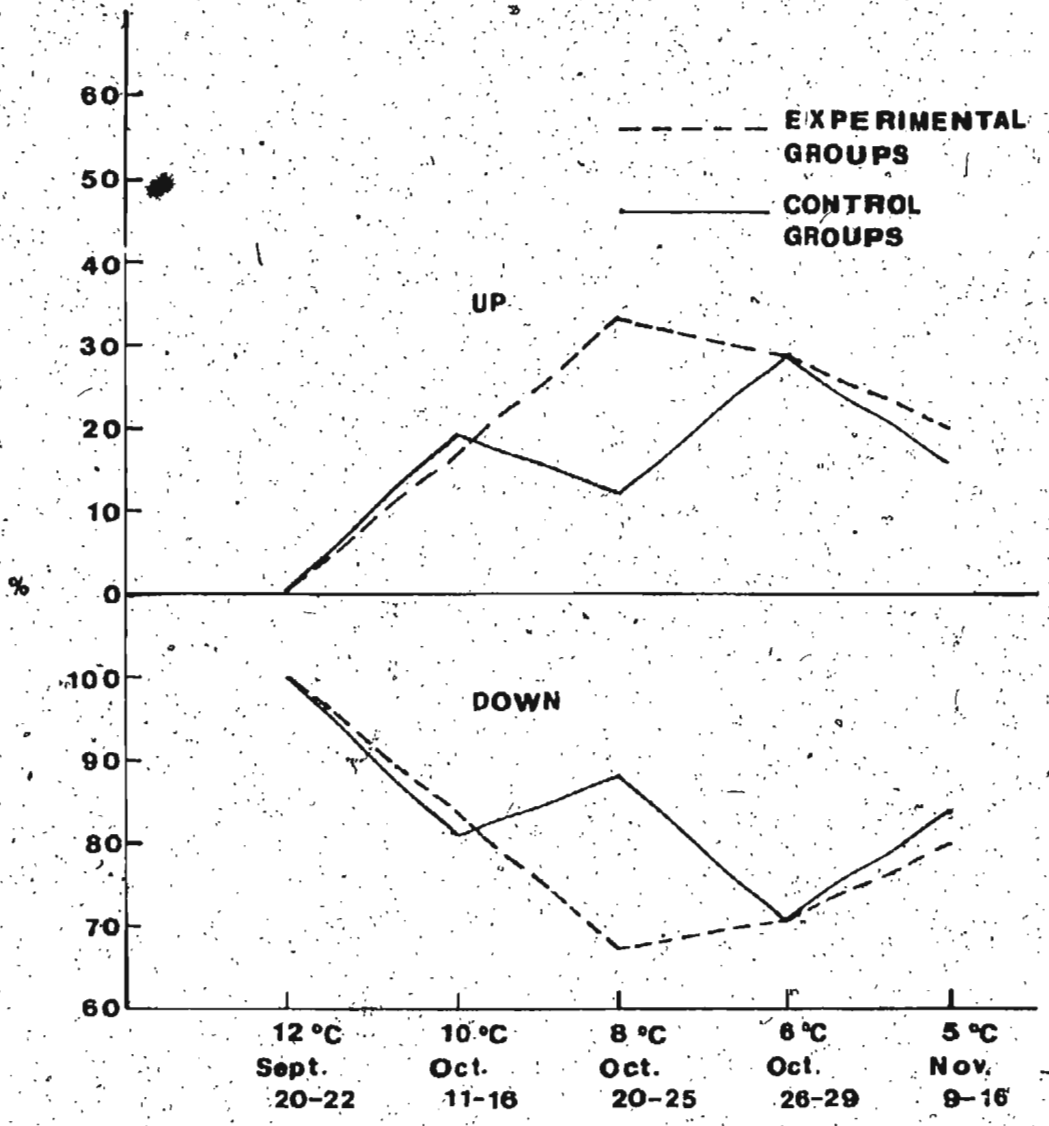
Table 7. Direction of movement of Northeast River mature male Atlantic salmon parr exposed to current, using replicate trials of three per subject.

Experimental							Control (12°C)						
Temp °C	Up	Down	P	No Response	No. of trials	No. of subjects	Date	Up	Down	P	No Response	No. of trials	No. of subjects
12[1]	0	10	< 0.001	20	30	10	Sept[1] 20-22	0	10	< 0.001	20	30	10
10	2	10	< 0.05	18	30	10	Oct 11-16	4	17	< 0.01	9	30	10
8	5	10	> 0.05	15	30	10	Oct 20-25	1	7	< 0.05	22	30	10
6	2	5	> 0.05	23	30	10	Oct 26-29	4	10	> 0.05	16	30	10
5	9	36	< 0.001	15	60	20	Nov 9-16	5	27	< 0.001	28	60	20
Total	18	71		91	180	60		14	71		95	180	60

$P < 0.001$ (Difference in upstream response between 12°C and 8°C)

[1] In this case the same data are presented twice; Data from 30 trials on 10 subjects represents results for both experimental and control groups.

Figure 7. Relationship of direction of movement to temperature and time for Northeast River precocious male parr.


EXPERIMENTAL GROUPS
CONTROL GROUPS
UP
DOWN
%
60
50
40
30
20
10
0
100
90
80
70
60
12 °C Sept. 20–22
10 °C Oct. 11–16
8 °C Oct. 20–25
6 °C Oct. 26–29
5 °C Nov. 9–16

highly significant ($P < 0.001$). It was for these October 20-25 trials that the greatest difference in directional responses occurred between an experimental group and controls.

As with the experimental groups, controls showed an increase in the upstream response later in the season. However, no distinct trend was apparent for the control groups. Only for October 11-16 trials was the upstream response more frequent for controls (19%) than for an experimental group (17% at 10°C).

Latency. The downstream response was significantly shorter at lower temperatures and later in the season ($P < 0.01$, Table 8, Figure 9). For controls, however, no significant relationship existed between $\log_{10}$ latency and time (Table 8, Figures 10-11). No significant relationship was found for the upstream response (Table 8, Figures 8, 10). Correlation was generally weak (r ranging from 0.14 to 0.40) and number of values for the upstream response was small (18 and 14 for experimental groups and controls respectively).

Southeast River parr:

Directional preference. The downstream response occurred significantly more frequently than did the upstream response for all but the precocious male experimental group (Table 9, Figure 12). Only for precocious males did the upstream response occur at all. The difference in occurrence of the upstream response between experimental groups of precocious males and immature parr was very highly significant ($P < 0.001$). The no response component was proportionately higher for immature parr than for precocious males (Figure 12).

Table 8. Mean latency of the response (sec.) of Northeast River mature male Atlantic salmon parr to current. (Means of $\log_{10}$ values and no. of observations in parentheses.)[1]

Sampling Day	Experimental			Control (12°C)	
	Temperature °C	Up	Down	Up	Down
1 (Sept. 19)	12		336 (2.4358) (10)		336 (2.4358) (10)
21 (Oct. 10)	10	71 (1.7460) (2)	199 (2.1075) (10)	53 (1.3527) (4)	232 (2.1796) (17)
30 (Oct. 19)	8	45 (1.5103) (5)	180 (2.0668) (10)	502 (2.7007) (1)	289 (2.2200) (7)
36 (Oct. 25)	6	243 (2.3738) (2)	169 (2.2170) (5)	69 (1.6532) (4)	219 (2.0221) (10)
50 (Nov. 8)	5	48 (1.3909) (9)	129 (1.7925) (36)	289 (2.1448) (5)	215 (2.1487) (27)

[1] Means were derived from replicate trials of three per subject on 10 parr except for Nov. 8 where samples were of 20 parr.

Figure 8. Relationship of latency of the upstream response to temperature for Northeast River precocious male parr.

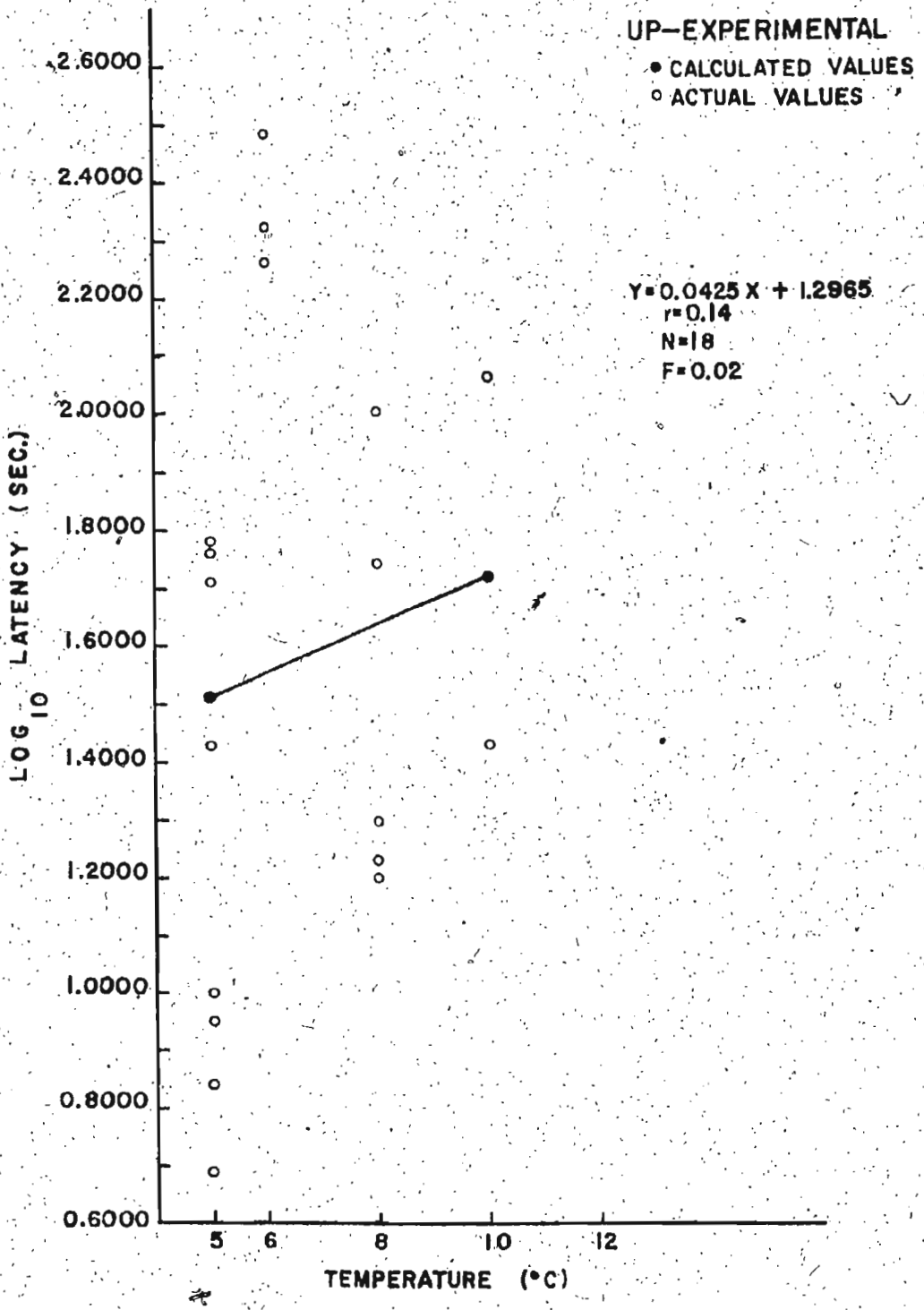

UP—EXPERIMENTAL
• CALCULATED VALUES
○ ACTUAL VALUES
Y=0.0425 X + 1.2965
r=0.14
N=18
F=0.02
LOG 10 LATENCY (SEC.)
2.6000
2.4000
2.2000
2.0000
1.8000
1.6000
1.4000
1.2000
1.0000
0.8000
0.6000
5
6
8
10
12
TEMPERATURE (°C)

Figure 9. Relationship of latency of the downstream response to temperature for Northeast River precocious male parr.

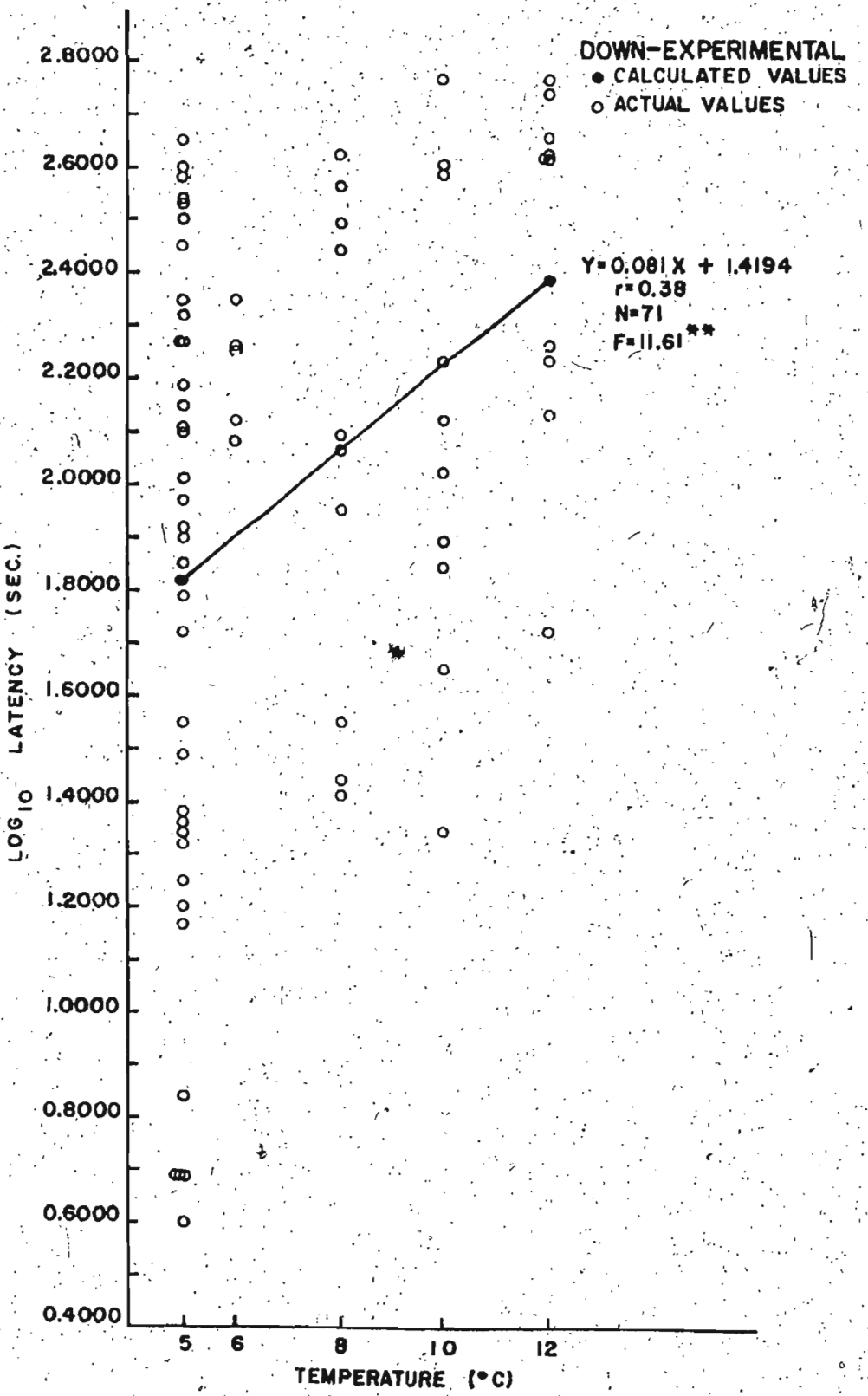

DOWN-EXPERIMENTAL
● CALCULATED VALUES
○ ACTUAL VALUES
Y=0.081X + 1.4194
r=0.38
N=71
F=11.61**
LOG10 LATENCY (SEC.)
2.8000
2.6000
2.4000
2.2000
2.0000
1.8000
1.6000
1.4000
1.2000
1.0000
0.8000
0.6000
0.4000
5
6
8
10
12
TEMPERATURE (°C)

Figure 10. Relationship of latency of the upstream response to time for Northeast River precocious male parr.

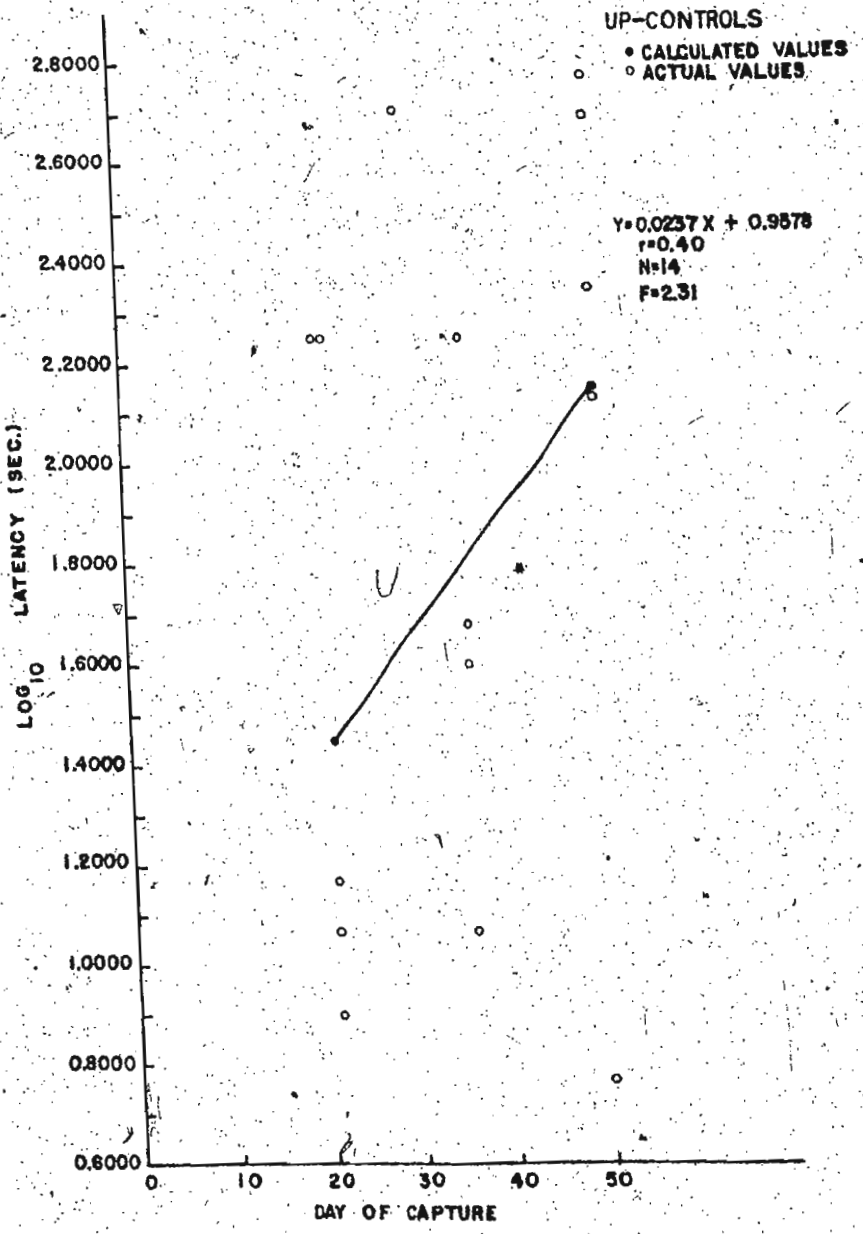

UP-CONTROLS
• CALCULATED VALUES
○ ACTUAL VALUES
Y=0.0237 X + 0.9578
r=0.40
N=14
F=2.31
LOG 10 LATENCY (SEC.)
2.8000
2.6000
2.4000
2.2000
2.0000
1.8000
1.6000
1.4000
1.2000
1.0000
0.8000
0.6000
0
10
20
30
40
50
DAY OF CAPTURE

Figure 11. Relationship of latency of the downstream response to time for Northeast River precocious male parr.

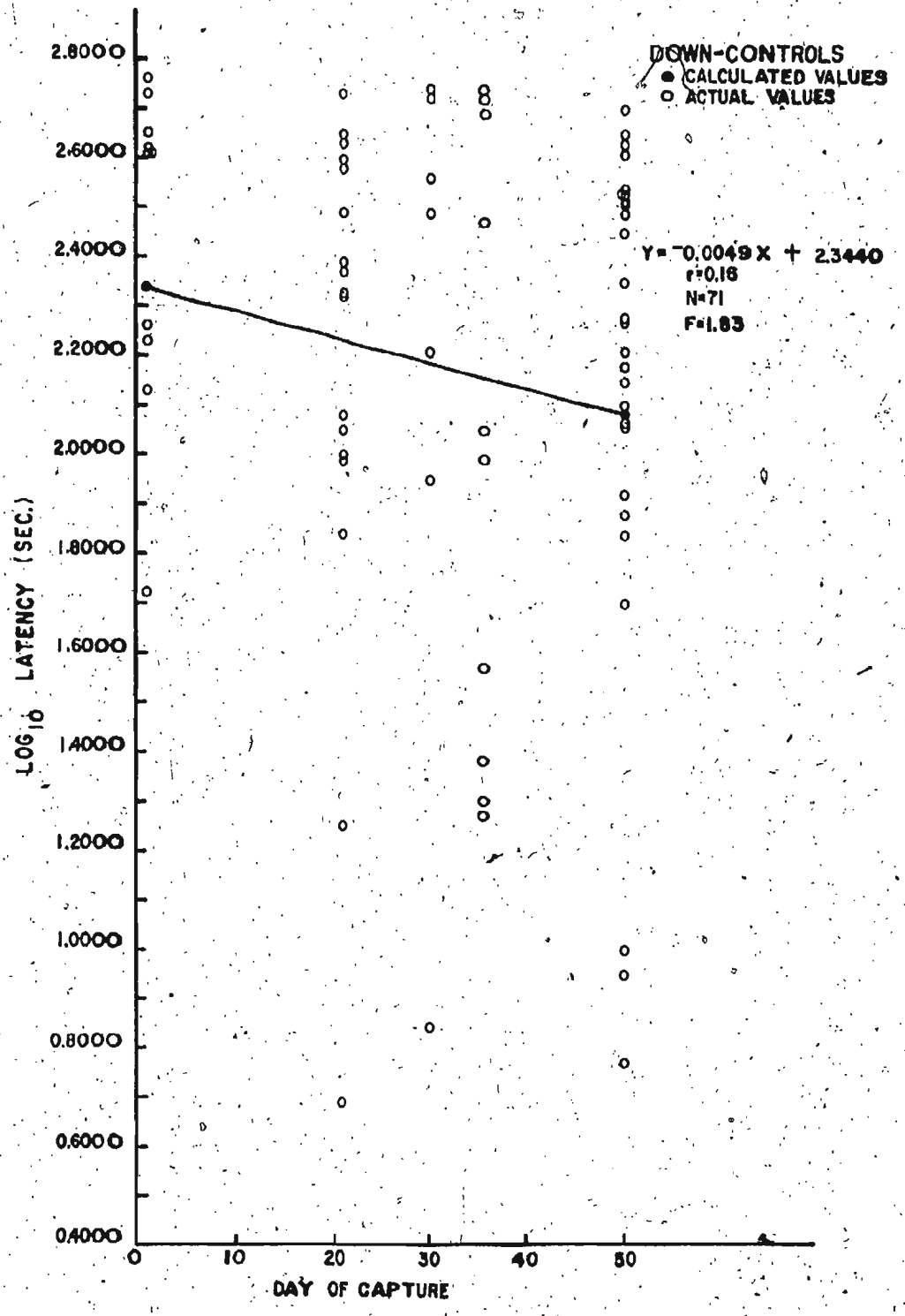
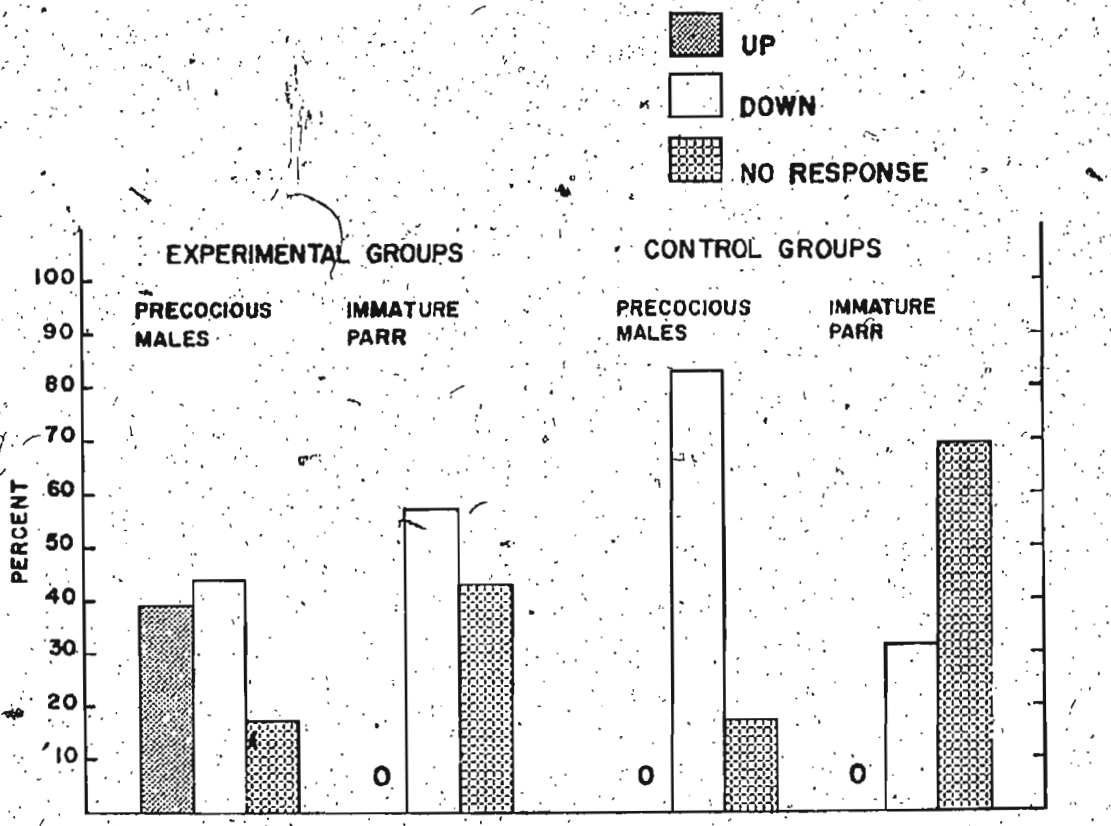

DOWN-CONTROLS
● CALCULATED VALUES
○ ACTUAL VALUES
Y = -0.0049 X + 2.3440
r=0.16
N=71
F=1.83
LOG10 LATENCY (SEC.)
2.8000
2.6000
2.4000
2.2000
2.0000
1.8000
1.6000
1.4000
1.2000
1.0000
0.8000
0.6000
0.4000
0
10
20
30
40
50
DAY OF CAPTURE

Table 9. Direction of movement of Southeast River Atlantic salmon parr exposed to current.

Sex and Maturity	Experimental (5°C)						Control (12°C)					
	Up	Down	P	No Response	No. of trials	No. of subjects	Up	Down	P	No Response	No. of trials	No. of subjects
Mature males	7	8	>0.05	3	18	6	0	5	<0.05	1	6	2
Immature parr	0	24	<0.001	18	42	14	0	20	<0.001	34	54	18
Total	7	32		21	60	20	0	25		35	60	20

$P < 0.001$ (Difference in upstream response for experimental precocious and non-precocious parr.)

Figure 12. Response to current of Southeast River parr at 5°C.


UP
DOWN
NO RESPONSE
EXPERIMENTAL GROUPS
CONTROL GROUPS
PRECOCIOUS MALES
IMMATURE PARR
PRECOCIOUS MALES
IMMATURE PARR
PERCENT
100
90
80
70
60
50
40
30
20
10
0
0
0

Latency. For experimental precocious males the upstream response was significantly faster than the downstream response ($P < 0.05$, Table 10). For both precocious males and immature parr no significant difference was found between experimental and control groups with respect to the downstream response.

Orientational component

Smolts

Positive orientation (heading into the current) occurred significantly more frequently for all but one set of conditions (Table 11). Only in freshwater and under conditions of ambient light intensity and 10°C was there no preference for positive orientation ($P > 0.05$). The most negative orientation occurred in freshwater, especially at 10°C. Ambient light intensity in general was associated with more negative orientation.

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For all parr negative orientation was generally more prominent (Tables 12 and 13). For Northeast River mature males this difference was highly significant for the 5°C experimental group and on October 20-25 and November 9-16 for controls ($P < 0.01$, Table 12). Significantly more negative orientation was also found for October 11-16 controls ($P < 0.05$). Only at 6°C for experimental precocious males and October 26-29 for controls was positive orientation more common.

For Southeast River parr negative orientation was consistently the more frequent, ranging from 70% to 100% (Table 13). This difference was significant for control precocious males ($P < 0.05$) and highly significant for experimental immature parr ($P < 0.01$).

Table 10. Mean latency of the response (sec.) of Southeast River Atlantic salmon parr to current. (Means of $\log_{10}$ values and no. of observations in parentheses)[1]

Sex and Maturity	Experimental			Control		
	Up	Down	t	Up	Down	t**
Mature males	38 (1.4775) (7)	144 (1.9137) (8)	1.8775*	171 (2.0524) (5)		0.4946
Immature parr		105 (1.7377) (24)		232 (1.9775) (20)		1.1284

* $P < 0.05$

** In this case t compares the downstream response between experimental and control groups.

[1] Means were derived from replicate trials of three per subject on eight mature male parr (six experimental, two control) and 32 immature parr (14 experimental, 18 control).

Table 11. Orientation of downstream response of Atlantic salmon smolts (percent in parentheses).

Salinity	Temperature	Orientation at Light Intensity: Dim +	Dim -	Dim P	Dim N*	Ambient +	Ambient -	Ambient P	Ambient N*
0 o/oo	10°C	16 (70)	7 (30)	<0.05	23	15 (50)	15 (50)	>0.05	30
	15°C	22 (96)	1 (4)	<0.001	23	18 (72)	7 (28)	<0.05	25
15 o/oo	10°C	16 (100)	0 (0)	<0.001	16	16 (89)	2 (11)	<0.01	18
	15°C	24 (100)	0 (0)	<0.001	24	32 (82)	7 (18)	<0.01	39
33 o/oo	10°C	21 (100)	0 (0)	<0.001	21	28 (100)	0 (0)	<0.001	28
	15°C	25 (96)	1 (4)	<0.001	26	32 (94)	2 (6)	<0.001	34

+ drifting passively while facing the current

- swimming actively with the current

N* is no. of downstream movements, derived from replicate trials on 20 smolts (three trials each at each combination of experimental conditions).

Table 12. Orientation of downstream response of Northeast River Atlantic salmon precocious male parr (percent in parentheses).

Experimental Temperature °C	Sampling Day	Orientation							
		Experimental				Control (12°C)			
		+	-	P	N*	+	-	P	N*
12	1 (Sept. 19)	4 (40)	6 (60)	>0.05	10	4 (40)	6 (60)	>0.05	10
10	21 (Oct. 10)	2 (20)	8 (80)	>0.05	10	4 (24)	13 (76)	<0.05	17
8	30 (Oct. 19)	5 (50)	5 (50)	>0.05	10	0 (0)	7 (100)	<0.01	7
6	36 (Oct. 25)	4 (80)	1 (20)	>0.05	5	7 (70)	3 (30)	>0.05	10
5	50 (Nov. 8)	9 (25)	27 (75)	<0.01	36	6 (22)	21 (78)	<0.01	27

+ drifting passively while facing the current

- swimming actively with the current

* In each case N is no. of downstream movements, derived from three trials on each parr. Samples were of 10 parr except for 5°C and controls where samples were of 20 each.

Table 13. Orientation of the downstream response of Southeast River parr at 5°C and controls (percent in parentheses).

Sex and Maturity	Orientation							
	Experimental (5°C)				Control (12°C)			
	+	-	P	N*	+	-	P	N*
Mature males	2 (25)	6 (75)	>0.05	8	0 (0)	5 (100)	<0.05	5
Immature parr	5 (21)	19 (79)	<0.01	24	6 (30)	14 (70)	>0.05	20

\+ drifting passively while facing the current

\- swimming actively with the current

* In each case N is no. of downstream movements, derived from replicate trials of three per subject on eight mature male parr (six experimental, two control) and 32 immature parr (14 experimental, 18 control).

DISCUSSION

Generally, juveniles displayed directional preference appropriate to known migration patterns. Downstream response was the more prominent for smolts, precocious male parr, and autumn immature parr. All experimental variables were found to affect rheotropic behavior in some way.

In any laboratory study caution must be exercised in interpreting results, due to existing unnatural experimental conditions. The downstream response could have been a fright reaction. However, this seems unlikely since subjects had five minutes to acclimate to test conditions before each trial. Also, responses were seldom immediate and the more frequent downstream response was generally associated with a longer latency. In any case, differences within experiments were accounted for by experimental variables and there was general agreement among results with respect to direction of movement, latency of the response, and orientation.

Kinetic component

Smolts

Directional preference:

By comparing results of the two smolt experiments for the same experimental conditions, the effect of holding smolts a longer time in the laboratory is seen. Extended captivity was associated with an increase in the frequency of the upstream response. However, for both experiments downstream was the more prominent directional response. Also, for both experiments, the upstream response was highest and the no

response component lowest in freshwater.

Significantly higher upstream response in freshwater may serve to retain smolts in ponds until the proper state of physiological readiness is attained (Allen 1944) or until favourable environmental conditions exist. Migration, once initiated, may remain intense as higher salinities are encountered.

Results of the second smolt experiment do not compare quantitatively with those of the first experiment. Both directional responses occurred more frequently in the second experiment, especially the upstream response. The no response occurred less frequently in the second experiment. However, these results are valid with respect to the effect of experimental variables. No single factor controlled rheotropic behavior but all factors considered affected it. The effects of these factors on rheotropic behavior were not independent.

As in the first smolt experiment, salinities above 0 o/oo were associated with an increase in the downstream response and a decrease in the upstream response. High upstream response in freshwater may be associated with maintaining smolts in nursery areas until they are physiologically ready to migrate. Increase in downstream movement with increased salinity may be associated with a commitment to seaward migration. Smolts drift passively with tidal currents in bays and estuaries (McCleave and LaBar 1976, McCleave 1977, Fried et al. 1978, LaBar et al. 1978). Such behavior may be related to acclimation to higher salinities. It is known that homing Atlantic salmon drift

passively with tidal currents along the coast near the home river (Hawkins et al. 1979) and in estuaries (Stasko 1975).

For combined salinities, ambient light intensity and the higher temperature were associated with most intense downstream movement. Ambient light intensity was associated with more downstream movement at all salinities, whereas the effects of temperature varied with salinity.

Ambient light intensity was of greater importance than higher salinities in increasing the intensity of downstream movement. Further, this effect of ambient light intensity was consistent at all salinities.

For freshwater this is supported by field observations on Northeast River (Dalley 1978) and other Placentia Bay rivers (O'Connell and Andrews, unpublished). Dalley and O'Connell and Andrews have found that diurnal migration was more intense than nocturnal movement at times of mass migration. This pattern of migration has been described by Bakshansky et al. (1976) for sub-polar rivers. Jessop (1975) reported a change from completely nocturnal migration early in the run to migration during the day as well for Big Salmon River, New Brunswick.

Greater downstream movement occurred under ambient light intensity at higher salinities. McCleave and LaBar (1976), McCleave (1977) and Fried et al. (1978) have shown using ultrasonic tracking that movement of smolts with the current in estuaries occurs in the day as well as night. Murray (1968) found for Little Codroy River that smolt catches from an estuarine trap reflected more intense diurnal than nocturnal

movement. Murray found that 83% of smolts entered the trap between 6 A.M. and 6 P.M. Between 6 A.M. and noon 47% was caught. That daytime downstream movement at greater salinities has been consistently reported may be related to less severe predation in the estuary and beyond.

In general, greater downstream movement at ambient light intensity suggests that seaward migration is a voluntary migration rather than a passive displacement due to the loss of visual cues as suggested by Hoar (1953).

The effect of temperature varied with salinity. In freshwater the lower temperature was associated with more downstream movement. Field observations by Dalley (1978) and O'Connell and Andrews (unpublished) show that the 1977 smolt runs for Placentia Bay rivers started when temperatures rose above 6°C and peaked before a minimum daily temperature of 10°C was reached. The exodus was virtually complete when morning temperatures reached 15°C. Other authors have reported smolt runs beginning at temperatures below 10°C (Osterdahl 1964, Bakshansky et al. 1976). Riche (1969) found for Long Harbour River 1966 that a continuous smolt run began after temperatures remained above 7°C. At 7°C smolts become active and begin to feed (Allen 1944).

Downstream movement in freshwater was low at the higher temperature. Perhaps this temperature is normally associated with downstream conditions which are unfavourable to survival or continued migration. Dominy (1973) suggested that when dowstream migration is delayed migration ceases and the

migratory urge wanes. In nature smolts which do not emigrate with the smolt run lose their silvery hue and revert to the parr condition (Evropeizeva 1958, Saunders 1960).

At a salinity of 15 o/oo more downstream movement was associated with the higher temperature whereas lower downstream movement occurred at 10°C. Perhaps at lower temperatures waiting occurs until optimum conditions for continued migration have been reached. It is known that smolt-migration is often delayed when they reach the estuary (Bull 1931, Stasko et al. 1973). Power (1969) found that Ungava Bay smolts do not leave the estuary until September or October, at which time the difference between river and sea temperatures is minimal.

Alternatively low estuarine temperature may not be responsible for suppressing continued migration. Rather 15°C may simply represent a later stage in the migration. Since the commitment to complete seaward migration has been made this higher temperature would enhance the response appropriate to this migration.

At 33 o/oo the higher temperature was associated with greater general responsiveness. The proportion of the downstream response was high for both temperatures. If such high salinities represent an advanced stage of migration then complete commitment to this migration may have been made. If this is so then environmental conditions such as temperature may not affect migration.

Latency:

Results for latency of the response in freshwater were generally in agreement with directional preference. The downstream response was faster at 10°C and ambient light intensity. Also, the downstream response was the faster in freshwater. In fact, the smallest value for $\log_{10}$ latency was recorded for the downstream response in freshwater at 10°C and ambient light intensity. It was also at these conditions that the greatest number of downstream responses occurred. The shorter latency of the downstream response in freshwater and ambient light intensity may be related to high predation during the daytime in the riverine portion of the seaward migration.

At higher salinities the latency of the response is not consistent with directional preference. The upstream response was significantly faster and there was no significant difference in response latency due to salinity or temperature. However, the latency of the response was generally faster for the ambient light intensity.

Parr

Northeast River precocious males:

Directional preference. The more frequent downstream response is in support of a downstream autumn migration of parr to overwintering areas. Also, this response may serve to maintain parr in ponds until environmental conditions are appropriate to the upstream spawning migration.

The frequency of the upstream response increased significantly to a maximum at 8°C on October 20-25. This is the approximate time and

temperature at which spawning occurs for Atlantic salmon on Northeast River. The first indication of spawning was on October 24 when three new redds were seen on the spawning ground above Junction Pond. River temperature was 8°C at 5 P.M. Time of spawning for Atlantic salmon is related to temperature. Jones and King (1949) found that spawning occurs within a temperature range of 36 - 47°F (2.2 - 8.3°C). Spawning time also depends on rapid cooling of river temperatures (Orton 1942, Smirnov 1971). Low occurrence of the upstream response may be related to the absence of adult females upstream, which serves as an important biological cue (King et al. 1939, Jones and King 1950, Buck and Youngson 1979).

Decrease in the upstream response and increase in the downstream response after October 26 and at lower temperatures for the experimental group is related to an increase in the number of daily downstream migrants later in the season (Smirnov 1971). Buck and Youngson (1979) found that the downstream migration of precocious male parr consistently began after and varied directly with the ascent of the first adult female. However, in one year where no adults were allowed to ascend, emigration occurred as usual. They suggested that some seasonal factor which releases emigration of precocious male parr is over ridden by the presence of adult females.

Latency. Regression analysis on latency of the response shows that only for the downstream response of the experimental group was a significant relationship found with time and temperature. The downstream response was significantly faster later in the season at lower temperatures.

This is consistent with increased intensity of downstream overwintering migration later in the season. Vladimirskaya (1958) reported that downstream movement of parr in autumn depends on the cooling rate of the water.

Southeast River parr:

Directional preference. Results for Southeast River parr are in agreement with those for Northeast River precocious male parr. The upstream response occurred only for precocious male parr where it occurred almost as frequently as did the downstream response. The highly significant difference between experimental groups of mature males and immature parr with respect to the upstream response is in agreement with the influence of water current as a directing mechanism in the upstream spawning migration of mature male parr. That no upstream response occurred for the precocious male control group is in agreement with the suggested importance of temperature in the timing of this migration. Exclusive occurrence of the downstream response for all but the experimental group of precocious males further supports the proposed role of water current in directing the downstream migration. Also, it suggests that sexual maturity is associated with reversing the response of male parr to current when optimally favourable environmental conditions for spawning occur. Buck and Youngson (1979) found that downstream migration of immature parr was controlled by season and occurred earlier than the descent of precocious males. Emigration of precocious males, even in the absence of spawning adults, occurred later. Hence it is likely that seasonal cues initiating downstream migration

function differently for immature parr and precocious male parr.

Latency. For the experimental group of Southeast River precocious males the upstream response occurred significantly faster than the downstream response. This is associated with an increase in the number of upstream responses at the time of spawning.

Field Observations:

In Northeast River traps were located near the inlet of Junction Pond. Parr catches from these traps yielded exclusively precocious male parr and in very high numbers. These ripe male parr seemed to congregate near the inlet until conditions were appropriate to upstream migration. Traps on Southeast River, however, were set near the outlet of Connaughtman's Pond. These traps yielded a lower catch of parr (40). Of these, 32 were found on later dissection to be immature parr and 8 were precocious males. Despite the fact that a spawning area was located directly below the outlet, it seems that all movement of precocious male parr, related to spawning, was upstream. Dalley (1978) found circumstantial evidence of an upstream spawning migration of precocious male parr in Northeast River.

Both spawning areas were electrofished immediately after spawning was completed and only one parr, a ripe male, was captured on Northeast River. Presumably mature males move downstream immediately after spawning (Smirnov 1971, Buck and Youngson 1979). Dalley (1978) found that numbers of parr on Northeast River spawning ground decreased shortly after spawning.

Orientational component

Smolts

Orientation of the downstream response of smolts was in close agreement with directional preference. More passive movement (positive orientation) occurred at salinities above 0 o/oo. This may be related to the possible role of passive drift in salinity acclimation. McCleave and LaBar (1976), McCleave (1977), Fried et al. (1978) found that smolts in the estuary move with tidal currents and at the same speed.

Also, more active movement (negative orientation) occurred at ambient light intensity. This is consistent with the significantly shorter latency of the response at this light intensity. More passive drift in dim light intensity may be related to passive displacement during twilight periods and at night, when smolts lose visual cues and cannot maintain position in the current (Hoar 1953).

Active movement occurred more frequently in freshwater. This may be related to the need for fast migration through the river because of the higher risk of predation. Negative orientation was most frequent in freshwater at 10°C and ambient light intensity. It was at these conditions that the downstream response was most frequent and had the shortest latency. Predation in the river would be more severe in the daytime.

Parr

Parr generally showed more active than passive downstream movement. This also may be related to the high risk of predation in the river.

Northeast River precocious males showed a higher incidence of passive movement about the times when upstream movement was more frequent. This may be related to a reluctance to move downstream at the time of spawning. However, in such cases few downstream responses occurred and it may be due to the low sample size.

SUMMARY

Rheotropic behavior was found to be consistent with field observations and known migration patterns. Downstream was the more common directional response for all juvenile Atlantic salmon.

Experimental variables interacted in regulating the response of smolts to current. Upstream response was more common in freshwater than at higher salinities. Latency of the downstream response was shorter where it occurred most frequently. Negative orientation of the downstream response was most common in freshwater, especially at the ambient light intensity. This may be related to potentially higher predation in the river, especially in the daytime. Passive drift (positive orientation), more common at higher salinities, may be related to acclimation to salinity.

Downstream response of parr was in support of a downstream overwintering autumn migration. Response of Southeast River control precocious males and immature parr was exclusively downstream. Upstream response of precocious male parr was related to an upstream spawning migration. For the Northeast River experimental precocious males, upstream response increased to the approximate temperature at which spawning occurs for Atlantic salmon. Also for this group, latency of the downstream response decreased later in the season and with lower temperatures. Parr generally showed negative orientation of the downstream response.

In conclusion, water current seems to serve as a directing mechanism in the migrations of juvenile Atlantic salmon. Environmental factors appear to have a role in regulating rheotropic responses appropriate to different seasonal migrations.

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